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JOURNAL OF THE EAST AFRICA NATURAL HISTORY SOCIETY AND NATIONAL MUSEUM

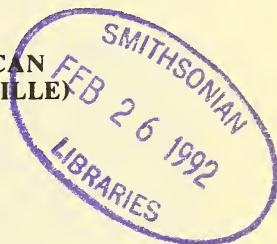
30 December 1982

No. 178

CHARACTERISTICS OF SWARMING IN THE AFRICAN
EDIBLE BUSH-CRICKET *RUSPOLIA DIFFERENS* (SERVILLE)
(ORTHOPTERA, TETTIGONIOIDEA)

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ABSTRACT

Previous reports on the African Edible Bush-cricket or 'nsenene', *Ruspolia differens* (Serville) (formerly *Homorocoryphus nitidulus* ssp. *vicinus* Walker), have left many questions unanswered as to the nocturnal behaviour of its swarms when uninfluenced by urban lights. Because large, dense swarms are widely known to arrive on hills at night it is tempting to infer that they traverse the skies in similarly compact formations. The present paper reviews the relevant background and reports new observations made on a massive swarm in the Shimba Hills of coastal Kenya, when no evidence of interaction between individuals was seen over the staggered post-sunset time of lift-off, and the swarm seemed unlikely to gain compactness through the insects' own behavioural responses since they showed no tendency to aggregate in flight. If these observations are widely valid, nocturnal compactness of rural *R. differens* swarms would seem to depend upon fortuitous characteristics of wind and topography acting upon intrinsically non-aggregative flight behaviour. Further reports are much needed.

INTRODUCTION

The African Edible Bush-cricket *Ruspolia differens* (Serville), now widely known by its Luganda name *nsenene*, is a slender insect some 4-6.5 cm in length with thread-like antennae of similar length. It occurs throughout the Afrotropical region including Madagascar, Mauritius, the Seychelles and the south-west Arabian Peninsula. It is among the very few species of Tettigonioidea which appear to form flying swarms of a high density, and where these swarms occur they are often gathered as a highly prized item of human food. Field studies on swarms together with reviews of previous literature are reported by Kevan & Knipper (1955) and Bailey & McCrae (1978).

The two main objectives of the present paper are to report new observations on the swarming of *R. differens* and to stimulate further investigations. Relevant details from previous studies are first summarised to provide the necessary context for the present and future reports, especially needed because these details are not widely known and particularly because some of the most telling observations on swarming may be of a negative nature.

Taxonomy

Bailey (1975) sank the former name *Homorocoryphus nitidulus* Scopoli ssp. *vicinus* Walker, replacing it with *Ruspolia differens* (Serville). In the same paper he described or redescribed several closely similar species, a few of which are widely sympatric with *R. differens* but none of which are known to swarm. All are indistinguishable in their larval stages, which makes field studies on the build-up of pre-swarming populations difficult.

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Colour forms

Six colour forms, all strikingly cryptic of the natural colours of grasses, occur in *R. differens*. The commonest are bright green (predominating in females) and straw-brown (more frequent among males than females). Scarcer morphs, not sex-linked in frequency, have purple either in longitudinal bands or, rarest of all, as a general suffusion of the head, thorax, upper abdomen and hind legs, superimposed on either green or brown (Owen, 1969; Bailey & McCrae, 1978). These six forms occur in all populations of *R. differens*, whether swarming or not, and therefore do not represent the colour/biological phases of true locusts or of Armyworm larvae.

Development, feeding and pest status

Eggs are laid in batches in the haulms of grasses where, under dry conditions, development is arrested at an early stage (anatrepsis) when they remain resistant to desiccation (Hartley, 1971). Development proceeds after wetting. At 30 °C and 50% RH it was found by Hartley (1967) that eggs hatched 11-12 days after wetting and the six larval instars developed in a further four weeks. In the field the late larval instars and adults evidently prefer a diet of anthers or, less so, the setting seeds of Gramineae (Kevan & Knipper, 1955; Swaine, 1964; Bailey & McCrae, 1978) so that their pest status with regard to grain crops such as rice, millet, sorghum and maize (Le Pelley, 1959; Swaine, *ibid.*) or to pasture (Kevan & Knipper, *ibid.*; Bailey & McCrae, *ibid.*) may be extensive but insidious and difficult to assess. In captivity they may eat grass leaves if a grain substitute is withheld, and if starved they may be cannibalistic.

Swarms and swarming behaviour

Swarming adults of *R. differens* contain much fat (Karuhize, 1972; Bailey & McCrae, 1978) and predisposition to the swarming state may therefore depend upon a high-nutrient diet rather than effects of population density. Seasonal development of grassland may therefore explain the seasonality of swarming (Bailey & McCrae, *ibid.*). Swarming usually follows after at least 1½-2 months of rain but does not necessarily coincide with actual rains. The heavier and more prolonged the rains, the larger and more persistent are the swarms, but there seems to be no carry-over of large swarms to the next season after dry conditions have intervened; that is to say, rainfall appears to influence the currently developing population and not survival to the next generation ahead.

Large swarms have occurred at lights in the Nairobi area in wetter years in May and more so in June (Kevan, 1947; Brown in Bailey & McCrae, 1978; Clifton, 1978) but it is not known whether the insects originate locally or from lower altitudes. Swarms are more frequent in the wetter and warmer climate of Uganda, with one or two swarming seasons per year in broad accord with local patterns of rainfall (Bailey & McCrae, *ibid.*).

In their sedentary state the individual adult insects spend the day low among grasses and if disturbed, either in the daytime or at night, they fly very little, but generally fall to the ground. In swarming seasons, daytime activity varies greatly. Dense aggregations which have arrived overnight in open grassland are usually static, the individuals flying short distances only on disturbance, or they may display spontaneous milling flights, more usual in wooded or thicket formations. In woodland this milling may take on a consistent direction unrelated to wind, the insects making short flights below treetop height. Swarms occasionally pass over water by day; one such was seen flying in from Lake Victoria at Mwanza in Tanzania during the hour before sunset in light drizzle, when the insects were widely spaced (Dr. R.M. Newson, pers. comm.). Small groups or individuals have been reported from ships far out to sea in the Gulf of Aden (Laird, 1962) and off West Africa (Steedman in Bailey & McCrae, 1978), the greatest offshore distance being 1210 km (Ragge, 1972). They are therefore capable of sustained flight by day if unable to land, but the distances to which large swarms rather than scattered individuals may be able to travel in this way remains equivocal.

Daytime flight thus seems at first sight to represent a behavioural continuum, but considering the evidence as a whole, the sedentary and swarming states appear distinct. In the swarming state, daytime flight behaviour is evidently influenced by ground cover and seems to depend on the relative brightness and 'grain' of fields of vision below, to the side and perhaps above the swarm.

On the subject of nocturnal flight away from the influence of artificial lights, information is very scanty. No low-flying masses of the insects have ever been reported flying across roads in the dark countryside, for example, which might imply that swarms normally travel at considerable height above ground, an interpretation perhaps supported by the fact that swarms often arrive at (and thus descend upon?) hills. It cannot be assumed, however, that the insects fly at night in a densely aggregated fashion at all; it is only known that they aggregate at sites of landing. Nocturnal observations conducted in towns may be misleading because lights will affect both the normal arrival and departure of swarms.

A conspicuous feature of urban swarms is their massed, sibilant male song at night (never by day), and similar song has been noted in rural situations, albeit on a smaller scale. The males then make intermittent bursts of sound at a steady rate of approximately 3 every 2 sec, in considerable synchrony. This 'swarm song' contrasts with the continuous song performed for up to 5 min or more by stationary males at low densities, which serves to attract females. The 'swarm song' involves inter-male aggression as well as much other activity by both sexes, but little if any mating. In other crickets and bush-crickets such intermittent song also commonly involves inter-male rivalry but serves for population spacing; in *R. differens* it appears to maintain swarm excitation, cohesion and perhaps recruitment. Since song can only be performed with the wings in a closed position, it cannot be produced in flight. The response of flying *R. differens* to massed 'swarm song' below them is a matter for conjecture, much in need of investigation.

Nocturnal observations on swarming behaviour away from the influence of lights pose special problems. An opportunity nevertheless arose very unexpectedly close to the Kenya coast in an area where swarms of *R. differens* had never before been noted, an account of which follows.

OBSERVATIONS

Description of swarm

A massive swarm of *R. differens* was first seen on the morning of 12 May 1982; it was absent on both the previous and the following days. It covered an area of at least 4 km² on some of the highest ground (360-450 m a.s.l.) of the Shimba Hills National Reserve, 20 km inland from the sea in coastal Kenya, stretching from Pengo Hill to the south-west flank of Longomagandi Forest (3° 22-26'E, 4° 14-15'S). The insects were distributed unevenly within this area; they were densest at and towards the topmost point of this part of the range, Pengo Hill, and in grasslands generally to the west of forest patches. They did not penetrate into forest. Maximum densities were estimated as approximately 20-25/ m².



Fig. 1 Part of a massive swarm of *R. differens* at the Shimba Hills National Reserve on 12 May 1982.

Weather conditions relevant to swarming

Light rain had fallen on the previous night when winds were moderate and westerly, abating towards dawn. At sea level on the coast the wind was easterly, suggesting convergence and turbulence on the eastern flank of the Shimbas. Thus, while the swarm may have accumulated through convergence, the direction from which it arrived was probably the west, in which case it is interesting that densities were greatest on upwind sides of forest.

Rains had commenced in the coastal area some six weeks before, and one to two weeks earlier than inland, just allowing time since putative break of egg diapause by wetting to account for a local origin of the swarm. Rains were exceptionally heavy for the three weeks prior to 12 May.

On 12 May in the swarm area, clouds and intermittent rain gave way to dry weather with intervals of weak sun by 1330h. The wind rose to a stiff south-west breeze by mid-morning, abating slightly at dusk.

Daytime swarm behaviour

During the day the swarm as a whole was static and the insects showed little if any spontaneous flight, nor were they seen climbing to flowering grass heads to feed. Unlike non-swarming populations, however, they flew readily on slight disturbance such as that caused by a vehicle passing close to roadside grasses. The auditory responses of the insects were particularly interesting. Shouting, whistling or clapping did not disturb them, but when a bunch of keys was shaken (emitting a wide sound spectrum including ultrasonic frequencies), many insects reacted with disturbance flights, rising up from as far away as 20 m. Individual flights were sustained for only about 3 sec, occasionally for up to 11 sec, which took them no higher than 4 m over open grassland. Followers were drawn up by those already disturbed until many were in flight together (Fig. 1), this over-all activity usually ending within 1 min of cessation of disturbance. This disturbance flight did not resolve itself into any consistent compass direction but merely extended outwards. When keys were shaken at the rate of 3 bursts of sound every 2 sec to simulate the 'swarm song', the insects still flew away from the source, not towards it.

Post-sunset swarm behaviour

For observations following sunset (at 1814h local time) a high-density site was chosen among tussocky grass 60-80 cm tall. The first insect to perform lift-off flight, i.e. sustained upward flight into the sky, was seen some 14 min after sunset but the next was not until 6 min later, after which the sky filled steadily with them. No male singing occurred and the insects appeared to rise from the grass at random; that is, no small foci of interaction or 'excitement centres' were discernible, nor was following induced, unlike the daytime disturbance situation.

Wind speed was 2-3 m/sec at 2 m height, as estimated by timed pacing of tobacco smoke. The insects faced into this wind as they flew and as they reached heights of 4-5 m they began to be blown slowly backwards, especially while rising, only making headway when diving steeply. Many individual insects were followed visually by means of 8x30 wide-angle binoculars and were seen to fly upwards until out of sight. They did not level off to form a denser layer at any particular height; they simply flew upwards and were dispersed.

The flying insects showed no interaction, neither forming clusters nor showing obvious avoidance of one another, either of which might have been expected had visual or auditory responses been engaged in interaction.

Lift-off flights continued at a more or less steady rate for as long as the insects could be seen against the brightest part of the sky. By 45 min after sunset at least half of them had still to fly, as judged by the numbers disturbed and seen by the headlights of a car then driven through the grassland. By next morning, few if any remained.

DISCUSSION

These observations indicate that nocturnal lift-off of swarming *R. differens* had little cohesion in either time or space. In time, lift-off was far from synchronous. In space, there seemed no clustering other than that brought about by characteristics of the swarm at its prior arrival. After lift-off there was no aerial layering, nor was there any indication that the insects would turn inwards and thus form up as the body of a flying swarm. It therefore seems questionable that the

insects traverse the skies in cohesive swarms, and until there is evidence to the contrary, nocturnal aggregations can only be claimed to occur as the insects come to land. The present observations suggest that their final aggregation would be determined by chance combinations of wind speed, wind direction and topography, coupled with the insects' landing responses.

To what extent may this be valid as a generalisation for the species? It might be argued that the observations were made when winds were too strong to permit swarm cohesion, and that below some threshold value which they might be capable of progressing against, the insects might orient differently on one another. This seems unlikely however, since they would still be moving at similar speeds relative to one another. It might alternatively be suggested that we were merely observing a swarm's dispersal by wind whereas in calm conditions they would mass themselves as they rose up, but there seems no reason why they would not merely continue to dilute their numbers in a vertical direction.

In conclusion, until nocturnal observations are reported on (a) lift-off flight under relatively windless conditions, (b) the height and densities of *R. differens* in full flight, and (c) their descent to the ground, then the view that *R. differens* travels at night in loose, non-interacting formations and not in cohesive swarms must remain the only tenable inference from existing data. Further observations are much needed and will depend upon alert opportunism.

ACKNOWLEDGEMENTS

I thank Dr. Michael Boppré and Dr. Bob Dransfield for information on conditions prior to and following my observations, and Mr. Christopher Dye for participating, and for providing Fig. 1.

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(Received 21 July 1982)

Joint Editors: M.E.J. Gore, Shereen Karmali

ROBERT HERBERT CARCASSON (1918-1982): AN APPRECIATION

Robert Carcasson was born on the 5th December 1918, in Cheltenham, and was educated in England and Italy. At the University of Florence's School of Tropical Agriculture (1935 to 1937) he obtained a diploma in tropical agriculture. In those same years he was fortunate in having the chance to learn the principles and methods of taxonomy from Roger Verity who at that time was compiling his monumental work on Italian butterflies.

With oral and written fluency in English, Italian and French, and a working knowledge of Spanish, Portuguese and Latin, the young man travelled in Africa and South East Asia between 1937 and 1939. In this period he studied zoology and worked in agriculture. With the commencement of World War II he joined up, and saw active service with the Rhodesian forces in Armoured Cars and Anti-Tank Artillery through East Africa, Ethiopia, Somalia, North Africa and Italy. Demobbed in 1946 he turned to pioneer farming on his own account in Rhodesia, which he did until 1955. In 1956 he returned to more academic pursuits and accepted the post of senior entomologist with Nairobi's Coryndon Museum. In 1961 he became the Museum's Director, combining this work with that of Senior Entomologist until 1968. During this period he worked towards, and was granted, a Ph.D by the University of East Africa for his studies on African Hawkmoths. He also added a fluency in Kiswahili to his linguistic accomplishments. In 1969 he became Chief Curator of the Centennial Museum, Vancouver, Canada. In 1971 he relinquished this post and travelled to Trinidad, Guyana and Brazil. In 1972 he travelled in Polynesia, Melanesia, Australia, Malaysia, Sri Lanka, Seychelles and East Africa in connection with the production of a Field Guide to Indo-Pacific Reef Fishes. Between 1973 and 1979 he was Curator of Entomology at the Museum of British Columbia.

From 1957 until 1980 he produced a more or less continuous stream of scientific papers. These ranged from records of new butterflies, through broad philosophical appreciations of the role of Natural History Museums in Tropical Africa to the beautifully illustrated book on Indo-Pacific Reef Fishes referred to above. Latterly he saw as the culmination of his work the publication (now in active preparation) of his "Synonymic Catalogue of the African Butterflies" by the British Museum. The curriculum vitae closes with his death from cancer in Victoria, B.C., Canada, on the 28th September 1982.

Although the above record is that of a remarkable man, it covers but a small part of his achievements and many abilities. His thinking on Africa's zoogeography influenced many and, in this field, he was entomology's counterpart to ornithology's Reg Moreau. While he was most widely known for his work with *Lepidoptera*, he was also an authority on coral reef fishes. But art was his field, too, and the record he left in his acrylic illustrations of butterflies, and fishes ranks him high among artists. As is so often the case with big men, his interests went far beyond those of his livelihood. Renaissance and Baroque music fascinated him and he never lost his love of farming. However, for all that he was an academic heavy-weight, the enduring memory of those who knew Bob Carcasson is of a warm personality with a keen sense of humour. In its simple and most complete sense, Bob was a thoroughly decent fellow. Our deepest sympathies go out to his wife Bee and son Francis. For all that Bob did not quite attain his three score and ten, he led a full life, he enjoyed it, and he extended human knowledge substantially enough to have a niche among the "greats" of Africa's natural historians. His memory is one to be proud of.

I.S.C.P.



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